

DISTRIBUTION AND SPECIES RICHNESS OF TREES IN SOUTHERN AFRICA*

R. S. KNIGHT, T. M. CROWE AND W. R. SIEGFRIED

(FitzPatrick Institute, University of Cape Town, Private Bag, Rondebosch 7700, R.S.A.)

ABSTRACT

A phytochorology for southern Africa is derived, based exclusively on species of trees. Cluster analysis, multi-dimensional scaling and information statistic tests are applied to isolate and characterize assemblages of tree species. Six major tree provinces, three of which contain a number of subprovinces, are recognized in a two-tier classification scheme. This phytochorology is compared with classification schemes based on subjective decisions and qualitative information. Correlation and regression analyses involving a suite of environmental variables are used in examining hypotheses concerning an increase in species richness with a decrease in geographical latitude, and a decrease in species richness with an increase in aridity.

UITTREKSEL

DISTRIBUSIE EN SPESIERYKHEID VAN BOME IN SUIDELIKE-AFRIKA*

In hierdie artikel word 'n fitochorografie vir Suider-Afrika voorgestel wat uitsluitlik gebaseer is op boomspecies. Groepe boomspecies word onderskei en gekarakteriseer deur middel van groeipanalises, multidimensionele gradering en die toepassing van statistiese inligtingstoetse. Ses hoofboomgebiede waarvan drie in aantal subgebiede insluit, word onderskei. Die voorgestelde fitochorografie word vergelyk met klassifikasiesistelsels wat op subjektiewe beslissings en kwalitatiewe informasie gebaseer is. Korrelasie- en regressieanalises wat 'n stel omgewingsveranderlikes behels, word gebruik om hipoteses oor 'n toename van spesierykheid met afnemende geografiese breedte en 'n afname van spesierykheid met toenemende dorheid te ondersoek.

INTRODUCTION

Southern African phytochorological studies (reviewed by Werger, 1978) tend to rely on unspecified data bases, and the criteria used to delimit phytochoria have frequently been undefined. Here we report a phytochorology for southern Africa based, for the first time, exclusively on trees, and modern analytical methods. In discussing the derived patterns of geographical

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distribution and species richness of the southern African tree flora, we examine hypotheses which have been advanced in explanations for the distribution of trees in other regions (Monk, 1967), or other major groups of plants or animals (Fischer, 1960; Williams, 1964; Pianka, 1966; Recher, 1971; Werger, 1978; McCoy and Connor, 1980). More particularly, we examine the following predictions: there should be an increase in species richness with a decrease in geographical latitude; and, there should be a decrease in species richness with an increase in aridity.

MATERIAL AND METHODS

The main data base was assembled from 1 362 distributional maps for indigenous tree species in Coates Palgrave (1977). These maps summarize records lodged at herbaria in southern Africa and represent the localities of occurrence enclosed within a continuous boundary, and cover all political states south of S 15°, except for Mozambique for which only the area south of the Zambezi River was included. Further, these maps do not represent an atlas of tree species but an aid to identification; however, they remain the only available source on tree distributions. With the concomitant increase in data base accuracy and resolution together with the refinement of analytical techniques (to increase data handling capabilities) the phytogeography for southern African trees based on quantified approaches will improve. A grid of 70 quadrats (Fig. 1) was used to transform each map into a numerical form; each quadrat being scored for each species according to a 1–10 scale, with each of the 10 numerals accounting for 10 % of the area of each quadrat and thus results in a 95 340 cell matrix.

Cluster analysis (Field and McFarlane, 1968; Anderberg, 1973) and multi-dimensional scaling (Kruskal, 1964) were used to identify groups of quadrats with similar species compositions. These two methods allow relatively objective and repeatable determination of potential patterns of sample grouping, based on all measured attributes (i.e. species) considered simultaneously and equally (Sneath and Sokal, 1973; Clifford and Stephenson, 1975). Information statistic tests (Field, 1969) were used to determine the species which characterize ($P < 0.01$) the groups of quadrats. The distribution of the most characteristic species was used in conjunction with the cluster analysis and ordination to produce a final pattern of tree assemblages. The species richness for each quadrat was subjected to a contouring programme (S. G. P. Diederiks, 1979) which fitted a surface, by a least squares polynomial analysis, to the data for visual representation.

Correlation and stepwise multiple linear regression analyses (Sokal and Rohlf, 1969; Allen, 1973) were used to determine possible relationships between species richness (the dependent variable) and ten measures of the en-

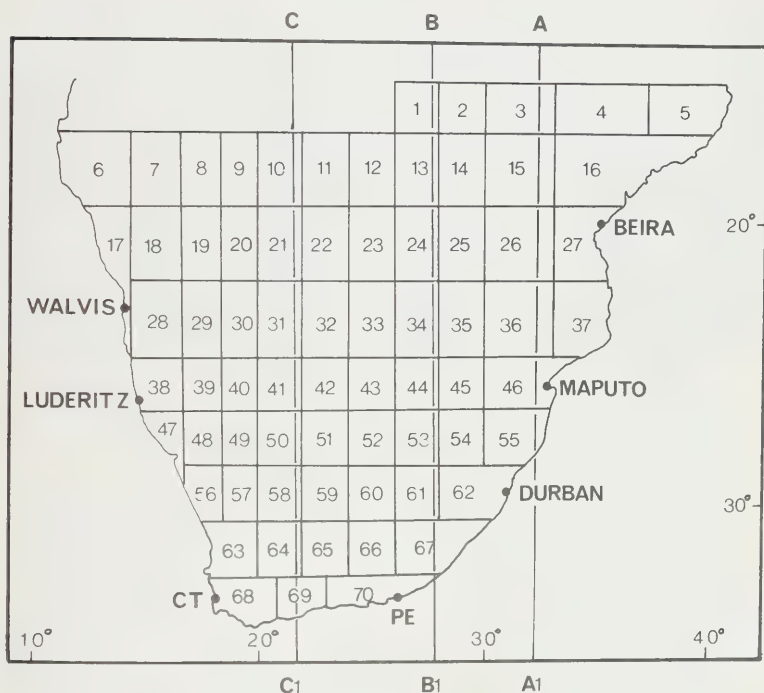


FIG. 1

The grid of quadrats (numbered 1–70) used in an analysis of the distribution of tree species in southern Africa. The lines A–A1, B–B1 and C–C1 represent transects (see Fig. 6).

environment (the independent variables): mean annual solar radiation (ANN-RAD); mean annual temperature (XTEMP); mean annual temperature range (TRANGE); January maximum temperature (TMAX); July minimum temperature (TMIN); mean annual rainfall (XRF); range in annual rainfall (RRANGE); altitudinal range (ARANGE); water surplus (WPLUS); and, actual evaporation (AE). These environmental data were taken from Talbot and Talbot (1960); Jackson (1961); Thornthwaite (1962); Clark (1967); and Schulze and McGee (1978).

RESULTS

A line drawn at the 20% similarity level across the dendrogram showing clusters of species assemblages (Fig. 2) separates six groups or provinces

(A–F), which were also distinct in multi-dimensional scaling (Fig. 3). Within three of these provinces, smaller clusters were identified between the 35 and 45 % similarity levels, and were designated as subprovinces (Figs. 2 & 3). The geographical boundaries of these areas are shown in Figure 4a. Figure 5 shows that species richness is relatively high in the eastern portion of the subcontinent, but there are few, if any, signs of an increase in species richness with a decrease in latitude (Fig. 6). Species richness is correlated positively and most strongly with mean annual rainfall (Fig. 7, Table 1). The second most strongly, though negatively, correlated environmental variable is mean annual solar radiation (Fig. 8, Table 1). The environmental variable with the second highest coefficient of determination is altitudinal range (Fig. 9, Table 1). Table 2 summarizes the results of the stepwise multiple regression analysis.

DISCUSSION

Phytochorology

Werger's (1978) phytochorology for southern Africa includes a Karoo-Namib region north of a Capensis subkingdom. He recognizes five domains within the Karoo-Namib region: Namib, Namaqualand, South Kalahari, Western Cape, and Karoo. In our subdivision of southern Africa, the Karoo province stretches much farther eastwards, but not as far northwards. Moreover, our Kalahari province is more distinctive, our belt along the Indian Ocean extends much farther inland, and Werger's (Fig. 4b) Namib region is split into northern and southern parts. There is also a minor difference, in that our Afro-montane Forest and Alpine Veld is more continuous than Werger's (Fig. 4b) and more closely approximates White's (1978) distribution of the division (Fig. 4c). White's Afro-montane archipelago includes two major assemblages for southern Africa, the Chimanimani in the north (comparable to our Zambezian Montane Forest) and the Drakensberg in the south (comparable to our Afro-montane Forest and Alpine Veld). However, unlike White's scheme, our eastern Karoo stretches to the western boundary of the Afro-montane Forest and Alpine Veld.

Other differences between White's scheme and ours are that he seems to have drawn little distinction between the Namib and the Karoo and in accordance with most other phytogeographers he does not recognize a separate Kalahari area.

Our phytochorological arrangement deviates from all other schemes in that we do not identify a strikingly distinct Capensis area; instead, we include a Capensis element at a second-order subprovince level. The main reason for this discrepancy rests in the selection of trees only for this study,

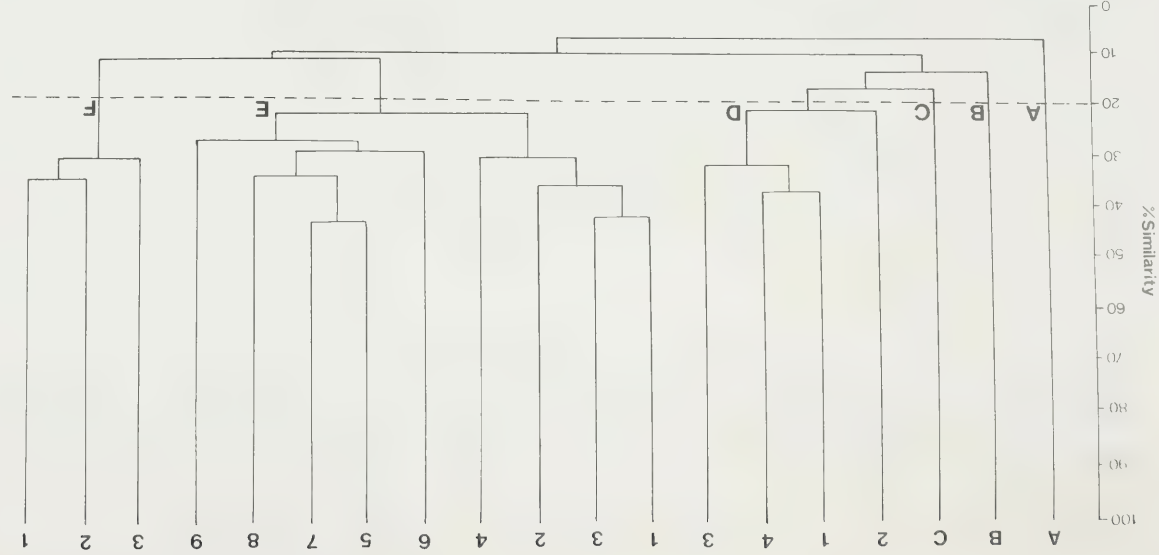


Fig. 2
The result of cluster analysis of 70 quadrats according to their tree species in southern Africa.

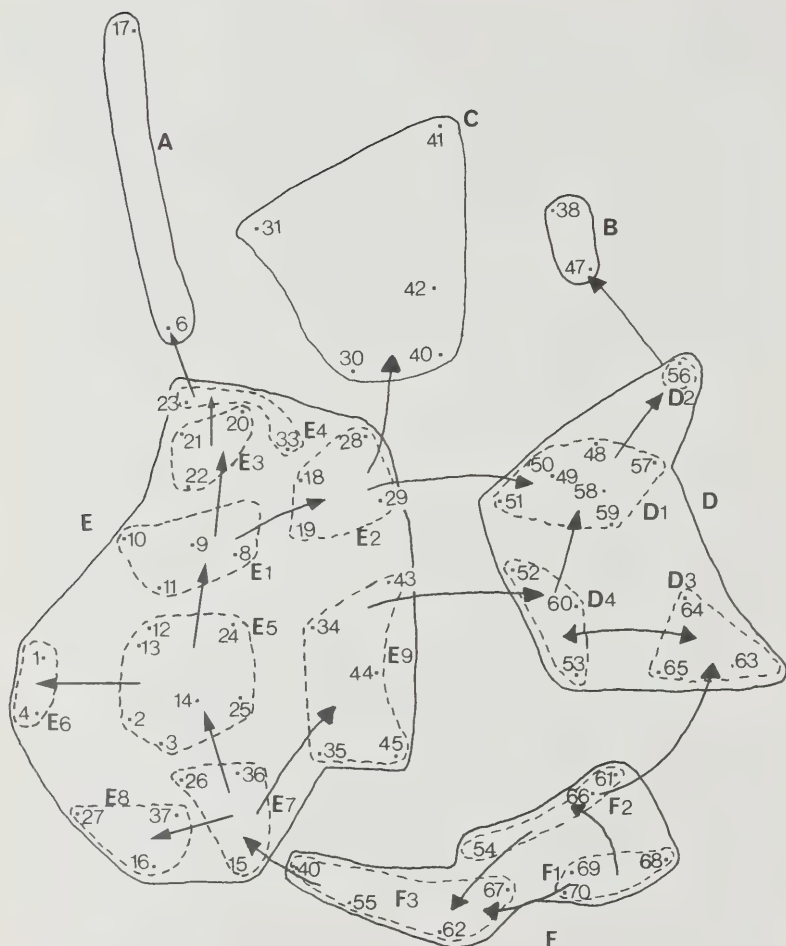


FIG. 3

The result of multi-dimensional scaling of 70 quadrats according to their tree species in southern Africa. The arrows indicate possible routes of species radiation.

TABLE 1

Correlation coefficient matrix of tree species richness and 10 environmental variables in southern Africa. SR = species richness, ANNRAID = annual solar radiation, XTEMP = mean annual temperature, TRANGE = annual temperature range, TMAX = maximum January temperature, TMIN = minimum July temperature, XRF = mean annual rainfall, RRANGE = annual range of rainfall, ARANGE = altitude range, WPLUS = water surplus, and AE = actual evaporation.

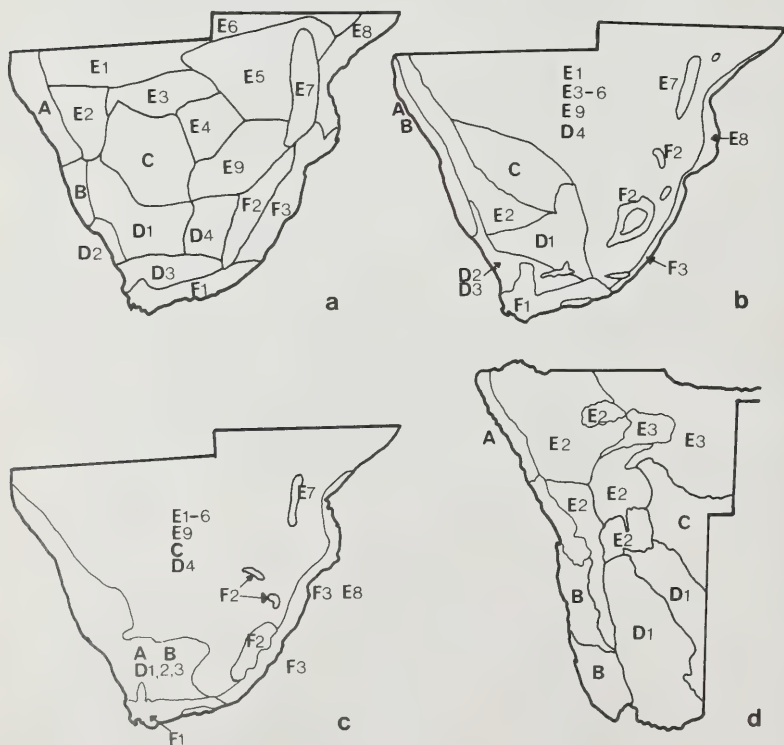
NAME	SR	ANNRAID	XTEMP	TRANGE	TMAX	TMIN	XRF	RRANGE	ARANGE	WPLUS	AE
SR											
ANNRAID	-0.622 *										
XTEMP	0.211	0.121									
TRANGE	-0.525	0.555	-0.106								
TMAX	0.143	0.342	0.484	0.551							
TMIN	0.273	-0.262	0.471	-0.756	-0.174						
XRF	0.641	-0.605	0.223	-0.400	-0.079	0.195					
RRANGE	0.527	-0.564	0.043	-0.499	-0.087	0.291	0.626				
ARANGE	0.492	-0.575	-0.456	-0.451	-0.560	0.038	0.301	0.403			
WPLUS	0.469	-0.459	0.247	-0.481	0.078	0.380	0.565	0.460	0.255		
AE	0.576	-0.531	0.177	-0.306	-0.136	0.107	0.942	0.552	0.250	0.290	

* Critical values of r for significance levels are: $r = 0.235$; $p = 0.05$; $r = 0.306$; $p = 0.01$.

TABLE 2

Results of stepwise regression analysis between quadrat tree species numbers and the environmental variables listed in Table 1 for southern Africa. XRF = mean annual rainfall, ARANGE = altitude range, XTEMP = mean annual temperature, and ANNRAD = mean annual radiation.

Variable	Coefficient of determination (R^2)	Regression Coefficient (Z)
XRF	0,41	0,41
ARANGE	0,50	0,07
XTEMP	0,59	22,96
ANNRAD	0,62	-2,77



thereby excluding the majority of the Capensis flora. However, there is also increasing evidence in favour of elements of the Capensis flora having affinities with the Alpine Veld of Lesotho (Killick, 1978).

The relatively large area of the Karoo province in our scheme may also be due to the selection of trees only. Trees are relatively sensitive to arid conditions, and all relatively dry areas may have been included in the Karoo simply because their trees are of a Karoo type, whereas the annual vegetation belongs to a different biotype. Although our Karoo, Kalahari and two Namib areas in South West Africa/Namibia do not conform with other generalized schemes (Fig. 4b), they do agree fairly closely with the vegetation types in Giess's (1970) map of the territory (Fig. 4d).

Biogeographical affinities

Our Central and South Namib (B) is the most distinct province, in that its closest point to its nearest neighbour is the farthest for any of the provinces (Fig. 3). Its closest neighbour, and therefore its closest affinities, could be with the Succulent West Coast Karoo (D2). Our Northern Namib (A) also has no very close affinities; the closest being with the Eastern Botswana Mopane subprovince (E4). It is surprising that the two provinces (Northern Namib and Central and South Namib) are quite so dissimilar, when geographically they lie adjacent to each other. The Kalahari (C) has strongest affinities with the Eastern Botswana Mopane (E4) and Thorn Tree Bushveld

FIG. 4

The proposed phytochorology compared to published phytochorologies. (a) Provinces (A-F) and subprovinces (1-9) found by cluster analysis and multi-dimensional scaling of the distribution of 1 362 tree species in southern Africa. The boundaries of the provinces and subprovinces are based on the individual distribution patterns of the 10 most characteristic species (see Appendix 1) being super-imposed on one another, and where intersections of 80 % or more occurred the intersection areas were enclosed in a continuous boundary. (b), (c) and (d) are redrawn maps of Werger's phytochorology (1976), White's phytochorology (1965, 1971), and Giess's phytochorology for South-West Africa/Namibia (1970) respectively. Each of these maps have our corresponding regions' names inserted to show the degree of compatibility. Names of the provinces and subprovinces:

A = Northern Namib, B = Central and South Namib, C = Kalahari, D = Karoo, E = Zambeziaca, F = Afro-montane and Coastal Forest, D1 = Arid Karoo, D2 = Succulent West Coast Karoo, D3 = Lower Mixed Veld Karoo, D4 = False Upper Karoo with Mixed Grassland, E1 = Combretum Tree Savanna and Woodland, E2 = Thorn Tree Bushveld, E3 = Mixed Acacia Bushveld, E4 = Eastern Botswana Mopaneveld, E5 = Matabele Tree Savanna and Woodland, E6 = Zambezi Mixed Tree Savanna and Forest, E7 = Zambezi Montane Forest, E8 = Mozambique Coastal Woodland and Savanna, E9 = Transvaal Mixed Bushveld, F1 = Capensis Montane Forest and Fynbos, F2 = Afro-montane Forest and Alpine Veld, F3 = Coastal Forest and Thornveld.

(E2) subprovinces, respectively. The Karoo (D) and Zambeziaca (E) provinces tend to be closest together at the Thorn Tree Bushveld (E2) and Arid Karoo (D1) subprovinces. The Afro-montane and Coastal Forest (F) province seems to have greatest affinities with the Zambeziaca (E) province, the most similar subprovinces between them being the Zambezian Montane Forest (E7) and the Coastal Forest and Thornveld (F3). This might be expected, since these areas experience similar temperature and rainfall regimes.

Southern Africa probably was covered by savanna and Cape sclerophyllous vegetation during the early Neogene (Axelrod and Raven, 1978). Alternating drought and wet periods are believed to have promoted enhanced plant speciation, in that during moist periods the sclerophyllous vegetation expanded into the present-day Karoo and speciated rapidly, whereas a coastward retraction occurred during dry conditions, leaving relict stands in the Karoo (Axelrod and Raven, 1978). Thus, relatively close affinities between the Karoo and Capensis might be expected. However, our Capensis Montane Forest and Fynbos (F1) subprovince is closest to the coastal forest and Thornveld (F3), and the whole of the Afro-montane and coastal Forest (F) province has affinities with a savanna, rather than a Karoo system (Fig. 3). Perhaps the onset of a dry climate and the forming of a Karoo system in its present position selectively excluded many trees, as opposed to relatively short-lived plants better able to escape the extremes of droughts. On this basis, it seems that our Karoo (D) province, with its dissimilar dominant species, represents a combination of the more xerophytic elements of the postulated former savanna and Cape sclerophyllous vegetation types.

During the Miocene the climate progressively became drier, restricting forest, while new vegetation forms, such as thorn scrub and grassland developed and savanna spread. Figure 3 shows that the Transvaal Mixed Bushveld (E9) subprovince has closer affinities with the Thorn Tree Bushveld (E2) than with its neighbouring Eastern Botswana Mopaneveld (E4). It seems likely that with increasing aridity the formerly continuous savanna between these two areas (E2 and E9) split, with the development of the Kalahari (C) in between and within the very dry interior basin.

A possible explanation of the dissimilarity between the adjacent Northern Namib (A) and Central South Namib (B) provinces might be that while the Northern Namib developed from the drier fringes of a tropical savanna, the Central South Namib developed at a later stage from the drier periphery of a then well-established Karoo system.

Species richness and environmental variables

Rainfall patterns for southern Africa demonstrate that the subcontinent is almost bisected by the 400 mm isohyet, with the eastern half considerably

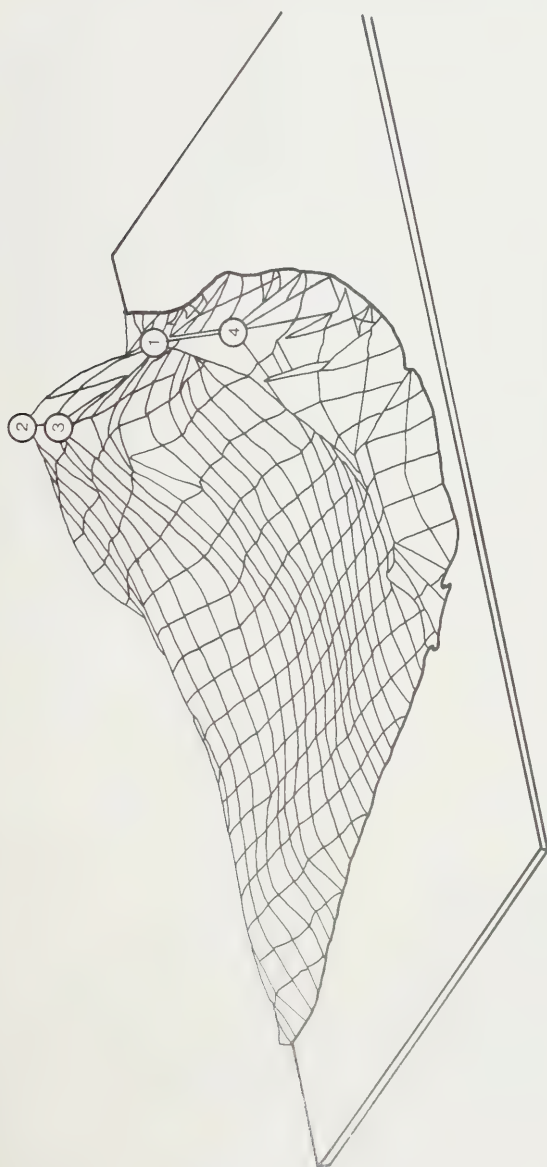


FIG. 5
Three-dimensional representation of the distribution of tree species richness in southern Africa (see Appendix 2). 1 = Komatipoort-Lebombo mountains (607 spp.), 2 = Vila Gouveia-Gorongosa (570 spp.), 3 = Haroni-Lusitu confluence (562 spp.), 4 = Zululand (554 spp.) are place names of areas with highest species richness.

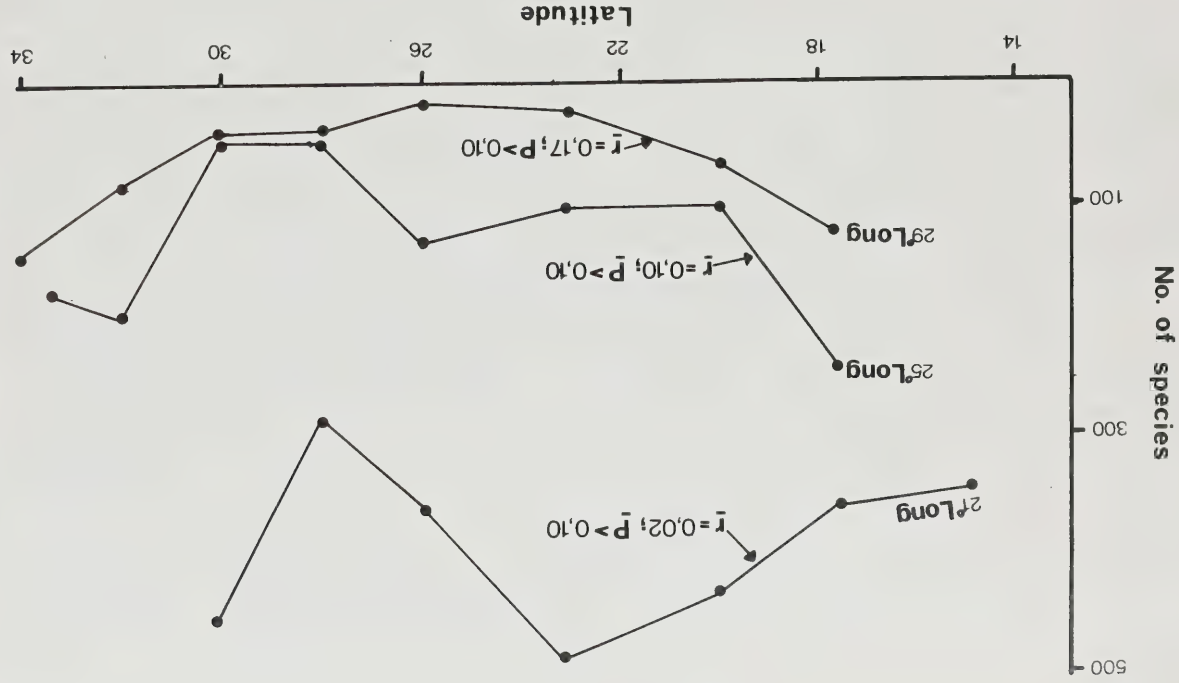


Fig. 6
Species richness of trees along three transects A-A1, B-B1 and C-C1 (see Fig. 1) in relation to latitude in southern Africa.

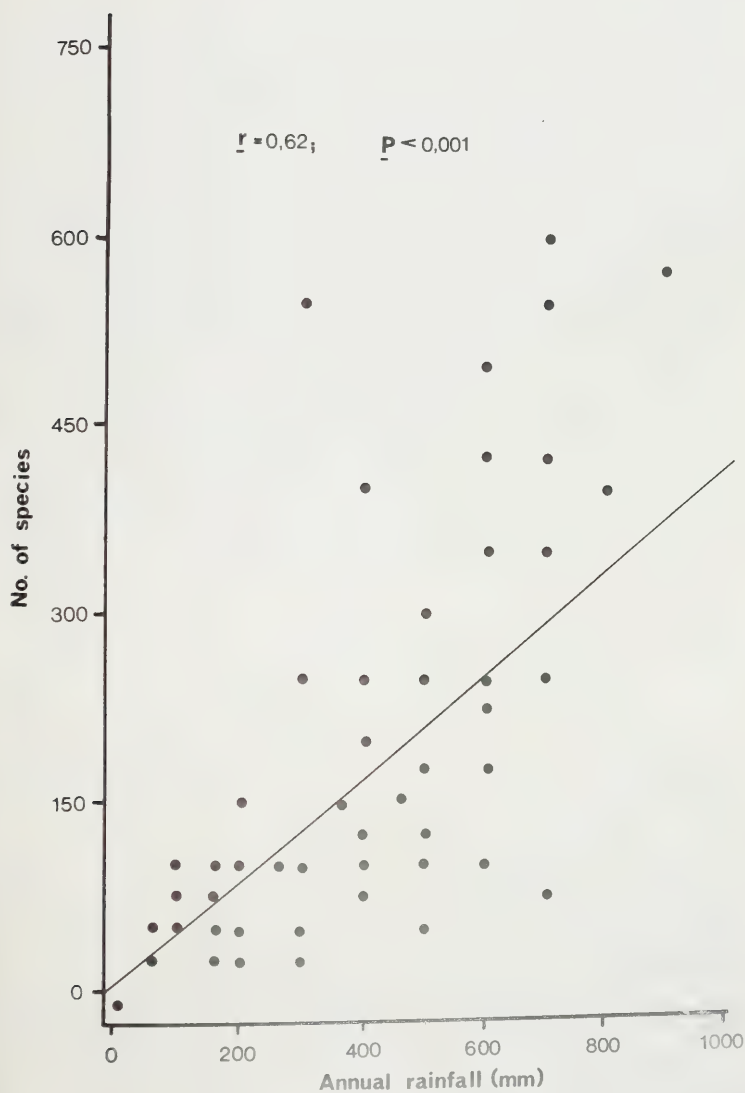


FIG. 7
Relationship between species richness of trees and mean annual rainfall in southern Africa.

moister than the western half (Jackson and Tyson, 1971). In general, tree species richness increases with increases in precipitation (Fig. 7), but it is probably more meaningful biologically to relate tree species richness to the extent of a positive difference between precipitation and water losses of the plants. Thus, a surprising result of our analyses is the low correlation between water surplus (WPLUS) and species richness (Table 1).

The intercorrelation between incoming solar radiation, temperature and precipitation, helps to explain why altitude range (ARANGE) has the second highest coefficient of determination in the multiple linear regression analysis (Table 1). In the stepwise regression analysis, only environmental variables which are not significantly correlated with those already in the regression equation can contribute to the regression (Allen, 1973). Thus, correlation and stepwise regression analysis are complementary statistical approaches (Crowe, 1979).

The most significant feature to emerge from the multiple characterization of each of our phytochorological provinces and subprovinces by environmental variables is that, areas with complex environments are not necessarily supportive of relatively high species richness. For instance, the Northern Namib province has great variability in temperature, rainfall and altitude, but the general aridity of the area apparently limits tree diversity, whereas other areas with less environmental diversity but higher rainfall support more species of trees.

Tropical biotas are thought to evolve and diversify relatively rapidly, because the tropics are less subject to widespread catastrophic events (e.g. glaciation) than temperate regions. On the other hand, the more heterogeneous and complex the physical environment becomes the more complex, and hence diverse, the biota becomes. The tropics are thought to be relatively heterogeneous and, therefore, to support more species than temperate regions. Thus, in essence, there are two lines of thought for explaining enhanced species richness in the tropics; and, they can be termed the "stability" and "heterogeneity" hypotheses, respectively.

If most of the variation in the species richness of the southern African tree flora could be linked with a combination of significant environmental variables, it could indicate subjectively a favouring of the "heterogeneity" hypothesis. For this to operate, the multiple regression analysis should have a high R^2 value (e.g. 0.85 or more). If, on the other hand, the variation in tree species richness is not only a function of present-day environmental variation, we would expect a much lower R^2 value (e.g. less than 0.66). We would interpret such a result to be consistent with a "stability" hypotheses, especially if the R^2 value was less than 0.50. Since the R^2 in the present study is 0.63, the most likely hypothesis is a mixed one. In other words, both environmental heterogeneity and stability have contributed to the observed

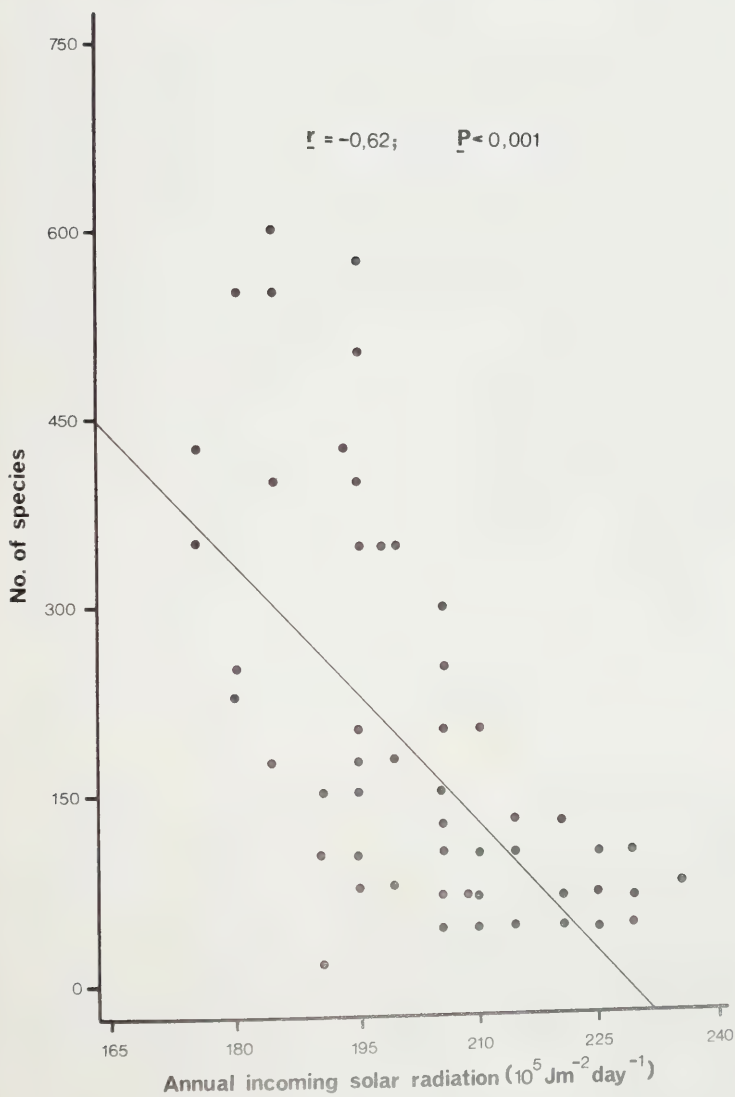
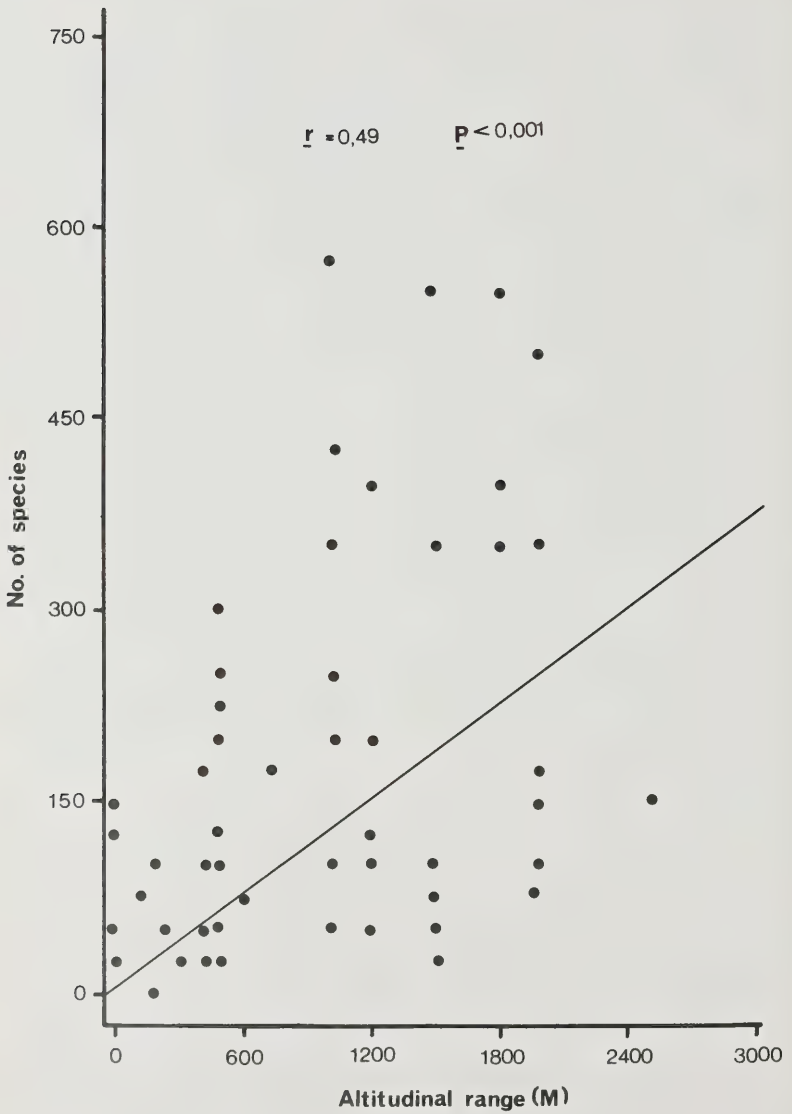


FIG. 8
Relationship between species richness of trees and mean annual solar radiation in southern Africa.



patterns of diversity. Moreover, those quadrats which have far more species than their present-day environmental heterogeneity would predict (e.g. quadrats 15, 26, 35 and 55; Figs 1 & 5 and Appendix 2) are, by inference, the most likely centres of stability. We predict that these centres of stability could have been "refugia" sensu Simpson and Haffer (1978).

Accepting that the subcontinent has been changing from a wet regime to a drier one, it is logical that the last areas to be directly affected would be protected gorges on the windward side of mountains. It is only in these areas that sufficient moisture can be retained for the support of past, "super-saturated", climax communities of trees, and therefore have an observed high species richness. Moreover, these communities are located in areas of high habitat diversity and thus would tend to conform to the "heterogeneity" hypothesis as well.

All four areas of exceptionally high species richness (Fig. 5) are characterized by a high diversity of habitat types. The Komatipoort area includes the moist, windward side of the Lebombo mountains and the southern Mozambique coastal plain, as well as the drier leeward side of the Lebombo range. The Vila Gouveia area includes the Gorongosa and Amatonga forests in the east, and well developed gallery forests along the streams of the Manica platform. East of Inyanga there are large Afro-montane forests and to the west a dominant moist deciduous woodland (*Brachystegia*) prevails. The Chipinga-Espungabera is the site of the Haroni-Lusita confluence and the steep descent of the Chimanimani mountains. It is here that high-altitude montane and high and low-altitude deciduous and riparian forests exist, as well as dry gallery forest along the Sabi river. Such a wide range of forest types within relatively small areas can be expected to yield high levels of richness in tree species.

CONCLUSIONS

This report shows that meaningful phytochorological results can be achieved through study of the distribution of tree species in southern Africa, using modern quantitative methods. The derived phytochorology has a great deal of compatibility with schemes based on subjective decisions and qualitative information. We propose a two-tier classification for assemblages of tree species, and suggest that some of the relationships between assemblages are the result of changes in vegetation patterns in the past. Evidence for tree species richness increasing with decreasing geographical latitude is not encouraging, whereas an hypothesis for an expected decrease in species richness with increasing aridity is acceptable. Apparently the balance between water input, in the form of rainfall, and water losses, linked with high solar radiation and temperature levels, is a critical factor determining the number of tree species in any given area. The sum of the environmental variables

studied cannot, however, adequately explain species richness variability and, therefore, other environmental factors that are not readily quantifiable (e.g., wind conditions), and/or historical factors, must be operating.

The results of our study apparently confirm Strahler's (1978) assertion that, "species groups tended not to be just groups with similar environmental preferences, but distinctive associations as well, with significance beyond their relationships to a particular site factor".

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APPENDIX 1

The 10 most characteristic ($P < 0.01$) tree species for each province and subprovince in southern Africa according to the information statistic test. Where there are fewer than 10 species for a province or a subprovince all the characteristic species are included.

Province A, Northern Namib

Species	2ΔI Value
<i>Commiphora wildii</i>	90,00
<i>Welwitschia mirabilis</i>	70,49
<i>Commiphora tenuipetiolata</i>	47,19
<i>Commiphora multijuga</i>	37,10
<i>Boscia tomentosa</i>	35,55

Province A, Northern Namib

Species	2ΔI Value
<i>Commiphora anacardiifolia</i>	29,51
<i>Commiphora kraeuseliana</i>	22,99
<i>Entandrophragma spicatum</i>	22,99
<i>Euphorbia eduardoi</i>	21,33
<i>Combretum wattii</i>	20,44

Province B, Central and South Namib

Species	2ΔI Value
<i>Parkinsonia africana</i>	55,71
<i>Ozoroa concolor</i>	21,98
<i>Cyphostemma bainesii</i>	15,73
<i>Tammarix usneoides</i>	7,27
<i>Rhus viminalis</i>	7,24
<i>Rauvolfia caffra</i>	5,93
<i>Pterocarpus rotundifolius</i>	5,60
<i>Commiphora capensis</i>	4,68
<i>Commiphora saxicola</i>	4,68

Province C, Kalahari

Species	2ΔI Value
<i>Ehretia rigida</i>	56,35
<i>Rhigozum brevispinosum</i>	27,82
<i>Ozoroa paniculosa</i>	17,61
<i>Combretum collinum</i>	15,14
<i>Acacia haematoxylon</i>	12,15
<i>Grewia flava</i>	10,20
<i>Catophractes alexandri</i>	8,95
<i>Acacia nebrownii</i>	5,49

Province D, Karoo

Species	2ΔI Value
<i>Nymaniania capensis</i>	192,50
<i>Rhus viminalis</i>	163,10
<i>Salix mucronata</i>	153,51
<i>Rhus undulata</i>	148,17
<i>Ozoroa dispar</i>	147,88
<i>Salsola aphylla</i>	124,04
<i>Maytenus linearis</i>	111,75
<i>Acacia haematoxylon</i>	102,38
<i>Cadaba aphylla</i>	91,34
<i>Aloe comosa</i>	88,46

Province E, Zambeziaca

Species	2ΔI Value
<i>Combretum imberbe</i>	238,00
<i>Burkea africana</i>	235,26
<i>Combretum hereroense</i>	219,51
<i>Peltophorum africanum</i>	208,02
<i>Securinea virosa</i>	202,94
<i>Dombeya rotundifolia</i>	195,59
<i>Commiphora africana</i>	191,35
<i>Combretum apiculatum</i>	184,09
<i>Piliostigma thonningii</i>	175,83
<i>Adansonia digitata</i>	171,90

Province F, Afro-montane and Coastal Forest

Species	2ΔI Value
<i>Rhus erosa</i>	256,88
<i>Clusia pulchella</i>	249,77
<i>Scolopia mundii</i>	243,26
<i>Scutia myrtina</i>	228,07
<i>Cassine peragua</i>	223,65
<i>Galpinia transvaalica</i>	214,74
<i>Rapanea melanophloeos</i>	214,56
<i>Maytenus acuminata</i>	210,59
<i>Chrysanthemoides monilifera</i>	206,35
<i>Burchellia bubalina</i>	204,81

Subprovince D1, Arid Karoo

Species	2ΔI Value
<i>Acacia haematoxylon</i>	64,03
<i>Boscia foetida</i>	53,32
<i>Aloe comosa</i>	35,33
<i>Adenolobus garipensis</i>	23,29
<i>Ozoroa namaensis</i>	22,63
<i>Acacia erioloba</i>	22,35
<i>Rhigozum brevispinosum</i>	21,32
<i>Salsola aphylla</i>	20,81
<i>Nymania capensis</i>	20,07
<i>Aloe littoralis</i>	18,85

Subprovince D2, Succulent West Coast Karoo

Species	2ΔI Value
<i>Aloe ramosissima</i>	45,33
<i>Ozoroa concolor</i>	28,33
<i>Euclea racemosa</i>	21,90
<i>Dideltia spinosa</i>	20,22
<i>Maerua gilgii</i>	19,90

Subprovince D2, Succulent West Coast Karoo

Species	2ΔI Value
<i>Euphorbia guerichiana</i>	18,09
<i>Ozoroa crassinervia</i>	16,89
<i>Aloe pillansii</i>	15,27
<i>Pachypodium namaquanum</i>	14,04
<i>Cotyledon paniculata</i>	8,03

Subprovince D3, Lower Mixed Veld Karoo

Species	2ΔI Value
<i>Chrysanthemoides monilifera</i>	41,69
<i>Dodonaea viscosa</i>	38,62
<i>Buddleja glomerata</i>	38,62
<i>Protea arborea</i>	32,18
<i>Phytica oleifolia</i>	32,18
<i>Phytica villosa</i>	32,18
<i>Rhus tomentosa</i>	28,97
<i>Hartogia schinoides</i>	28,97
<i>Kiggelaria africana</i>	27,74
<i>Diospyros glabra</i>	25,75

Subprovince D4, False Upper Karoo with Mixed Grassland

Species	2ΔI Value
<i>Rhus leptodictya</i>	48,65
<i>Euclea crispa</i>	48,63
<i>Ilex mitis</i>	47,33
<i>Ficus soldanella</i>	46,87
<i>Protea caffra</i>	46,87
<i>Celtis africana</i>	44,95
<i>Cussonia paniculata</i>	43,52
<i>Carissa bispinosa</i>	43,52
<i>Diospyros whyteana</i>	41,28
<i>Rhus pyroides</i>	40,27

Subprovince E1, Combretum Tree Savanna and Woodland

Species	2ΔI Value
<i>Grewia schinzii</i>	96,79
<i>Combretum engleri</i>	65,24
<i>Ozoroa longipes</i>	61,35
<i>Combretum psidioides</i>	49,96
<i>Combretum celastroides</i>	46,77
<i>Steganotaenia araliacea</i>	43,23
<i>Pachypodium lealii</i>	42,72
<i>Bridelia tenuifolia</i>	38,91
<i>Bauhinia urbaniana</i>	35,02
<i>Entandrophragma spicatum</i>	35,02

Subprovince E2, Thorn Tree Bushveld

Species	2ΔI Value
<i>Ozoroa crassinervia</i>	110,57
<i>Moringa ovalifolia</i>	95,43
<i>Euclea pseudebenus</i>	90,20
<i>Cyphostemma currorii</i>	83,82
<i>Ficus cordata</i>	77,73
<i>Boscia foetida</i>	77,73
<i>Ficus ilicina</i>	74,08
<i>Montinia caryophyllacea</i>	73,74
<i>Vernonia cinerascens</i>	72,98
<i>Commiphora tenuipetiolata</i>	69,92

Subprovince E3, Acacia Bushveld

Species	2ΔI Value
<i>Lonchocarpus nelsii</i>	26,09
<i>Acacia fleckii</i>	24,98
<i>Grewia retinervis</i>	15,99
<i>Combretum collinum</i>	15,52
<i>Catophractes alexandri</i>	13,28
<i>Commiphora angolensis</i>	11,49
<i>Rhus tenuinervis</i>	9,98
<i>Commiphora africana</i>	7,28
<i>Bauhinia petersiana</i>	6,84
<i>Hibiscus diversifolius</i>	4,91

Subprovince E4, Eastern Botswana Mopane

Species	2ΔI Value
<i>Colophospermum mopane</i>	9,77
<i>Catophractes alexandri</i>	8,45
<i>Albizia harveyi</i>	5,82
<i>Grewia tenax</i>	4,78
<i>Hyphaene benguellensis</i>	4,53
<i>Acacia nebrownii</i>	4,15

Subprovince E5, Matabele Savanna and Woodland

Species	2ΔI Value
<i>Vepris zambesiaca</i>	119,81
<i>Cassia singueana</i>	111,33
<i>Euphorbia matabelensis</i>	108,60
<i>Boscia angustifolia</i>	99,85
<i>Azanza garckeana</i>	97,72
<i>Combretum elaeagnoides</i>	94,70
<i>Commiphora mossambicensis</i>	92,63
<i>Elephantorrhiza goetzei</i>	85,47
<i>Dalbergia melanoxylon</i>	76,65
<i>Pterocarpus rotundifolius</i>	76,28

Subprovince E6, Zambezan Mixed Tree Savanna and Forest

Species	2ΔI Value
<i>Rhodognaphalon schumannianum</i>	22,89
<i>Triplochiton zambesiacus</i>	20,48
<i>Schrebera trichoclada</i>	14,96
<i>Leptactina hexamera</i>	11,44
<i>Diospyros squarrosa</i>	10,60
<i>Tamarindus indica</i>	10,57
<i>Monotes engleri</i>	10,10
<i>Uapaca nitida</i>	9,52
<i>Cola mossambicensis</i>	9,43
<i>Allophylus africanus</i>	8,37

Subprovince E7, Zambezan Montane Forest

Species	2ΔI Value
<i>Cassia petersiana</i>	66,12
<i>Acacia xanthophloea</i>	61,50
<i>Androstachys johnsonii</i>	58,20
<i>Stadmania oppositifolia</i>	56,84
<i>Breonadia microcephala</i>	53,73
<i>Strychnos mellodora</i>	49,13
<i>Xeromphis rudis</i>	47,98
<i>Rinorea elliptica</i>	47,34
<i>Trichilia emetica</i>	46,71
<i>Thilachium africanum</i>	46,60

Subprovince E8, Mozambique Coastal Woodland and Savanna

Species	2ΔI Value
<i>Casearia gladiiformis</i>	85,22
<i>Enterospermum littorale</i>	78,62
<i>Coffea racemosa</i>	69,86
<i>Diospyros rotundifolia</i>	68,78
<i>Drypetes natalensis</i>	66,09
<i>Pseudobersama mossambicensis</i>	63,87
<i>Tarenna junodii</i>	63,79
<i>Ochna natalita</i>	60,50
<i>Sonneratia alba</i>	58,96
<i>Avicennia marina</i>	58,96
<i>Barringtonia racemosa</i>	58,96

Subprovince E9, Transvaal Mixed Bushveld

Species	2ΔI Value
<i>Buddleja saligna</i>	115,33
<i>Aloe marlothii</i>	114,70

Subprovince E9, Transvaal Mixed Bushveld

Species	2ΔI Value
<i>Acacia caffra</i>	112,42
<i>Commiphora neglecta</i>	106,17
<i>Solanum giganteum</i>	100,84
<i>Berchemia zeyheri</i>	100,35
<i>Nuxia congesta</i>	92,59
<i>Canthium suberosum</i>	89,51
<i>Cussonia paniculata</i>	87,39
<i>Protea caffra</i>	85,62

Subprovince F1, Capensis Montane Forest and Fynbos

Species	2ΔI Value
<i>Rhus incisa</i>	72,23
<i>Atalaya capensis</i>	72,23
<i>Cassine parvifolia</i>	67,42
<i>Freylinia lanceolata</i>	65,01
<i>Lachnostylis hirta</i>	62,60
<i>Hartogia schinoides</i>	58,70
<i>Maytenus oleoides</i>	57,79
<i>Protea arborea</i>	57,79
<i>Euclea racemosa</i>	50,10
<i>Olea exasperata</i>	49,85

Subprovince F2, Afro-montane Forest and Alpine Veld

Species	2ΔI Value
<i>Rhus transvaalensis</i>	73,46
<i>Rhus erosa</i>	37,57
<i>Calpurnia robinoides</i>	28,89
<i>Rhus montana</i>	21,67
<i>Protea caffra</i>	19,26
<i>Euphorbia curvirama</i>	12,04
<i>Euclea coriacea</i>	11,97
<i>Leucosidea sericea</i>	9,15
<i>Cussonia paniculata</i>	8,90
<i>Erica caffrorum</i>	8,84

Subprovince F3, Coastal Forest and Thornveld

Species	2ΔI Value
<i>Vitellariopsis marginata</i>	58,64
<i>Dombeya cymosa</i>	54,97
<i>Turraea floribunda</i>	54,97
<i>Euphorbia tirucalli</i>	54,24
<i>Brachylaena ilicifolia</i>	51,31
<i>Bersama lucens</i>	51,31

Subprovince F3, Coastal Forest and Thornveld

Species	2ΔI Value
<i>Nuxia congesta</i>	50,70
<i>Tricalysia capensis</i>	48,93
<i>Cussonia sphaerocephala</i>	47,64
<i>Diospyros villosa</i>	47,64

APPENDIX 2

The number of tree species in the quadrats shown in Fig. 1.

No.	Spp.	No.	Spp.	No.	Spp.	No.	Spp.	No.	Spp.
1	242	15	570	29	93	43	117	57	59
2	342	16	355	30	46	44	180	58	44
3	409	17	20	31	26	45	349	59	33
4	181	18	112	32	13	46	607	60	51
5	1*	19	109	33	96	47	25	61	95
6	90	20	57	34	209	48	60	62	49
7	142	21	62	35	494	49	53	63	74
8	126	22	103	36	395	50	41	64	65
9	121	23	96	37	233	51	41	65	94
10	113	24	238	38	27	52	55	66	202
11	189	25	434	39	63	53	85	67	359
12	238	26	562	40	31	54	258	68	148
13	295	27	251	41	13	55	554	69	160
14	352	28	95	42	30	56	44	70	187

* Excluded from the multivariate analysis as most of it fell outside the range of the maps used in Coates Palgrave.